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Epigaeic ant diversity and distribution in the Sandstone Sourveld in KwaZulu-Natal, South Africa

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Abstract

Ants are sensitive to habitat change and may be affected by disturbances, such as alien plant invasion. Alien plant invasion is associated with negative effects on the functioning of ecosystems and may have adverse impacts on biodiversity. The aim of this study was to determine the diversity of ground-dwelling ants in Tanglewood and Giba Gorge Reserves in KwaZulu-Natal Province, South Africa. Ants were sampled in the wet and dry seasons. Pitfall trap sampling was carried out in an intact grassland, forest and a disturbed grassland. We collected 360 samples resulting in a total of 2,577 occurrences comprising of 54 species. We found that diversity of ants in the two sites was influenced by vegetation type. The intact grassland in the two reserves had greater diversity (40 ± 4.45) of ants compared with forest (22 ± 4.86) and disturbed grassland (27 ± 1.15); however, the disturbed grassland supported higher ant occurrences (50.03 \pm 31.6). Opportunists represented the most diverse functional group with 17 species followed by specialist predators with 13 species and generalised Myrmicinae with 10 species. These results suggest that grassland disturbance by alien plant invasion provides suitable environmental conditions that may increase ant occurrences but decrease ant diversity.

Abstrait

Les fourmis sont sensibles au changement d'habitat et peuvent être affectées par des perturbations, telles quelles, l'invasion de plantes étrangères. L'invasion des plantes étrangères est liée à des effets négatifs sur le fonctionnement des écosystèmes et peut avoir des effets négatifs sur la biodiversité. L'objectif de cette étude était de déterminer la diversité des fourmis terrestres dans les réserves de Tanglewood et de Giba Gorge dans la province du KwaZulu-Natal, en Afrique du Sud. Les fourmis ont été testées pendant la saison humide et sèche. Un échantillonnage de pièges a été réalisé dans une prairie intacte, une forêt et une prairie perturbée. Nous avons recueilli 360 échantillons, causant un total de 2577 occurrences comprenant 54 espèces. Dans les deux sites, nous avons constaté que la diversité des fourmis était influencée par le type de végétation. Les prairies intactes des deux réserves présentaient une plus grande diversité (40 ± 4,45) de fourmis dans les prairies forestières (22 ± 4,86) et perturbées (27 ± 1,15), cependant les prairies perturbées supportaient des occurrences de fourmis plus élevées (50,03 ± 31,6). Les opportunistes représentaient le

groupe fonctionnel le plus diversifié avec 17 espèces, suivis par des prédateurs spécialisés avec 13 espèces et des Myrmicinae généralisées avec 10 espèces. Ces résultats suggèrent que la perturbation des prairies par l'invasion de plantes étrangères fournit des conditions environnementales appropriées pouvant augmenter les occurrences de fourmis mais diminuer la diversité des fourmis.

KEYWORDS

abundance, alien plant invasion, grassland, ground-dwelling ants, vegetation type

1 | INTRODUCTION

Ants (Hymenoptera: Formicidae) are among the most dominant and diverse groups of arthropods on earth (Guenard, 2013; Sonune & Chavan, 2016) and are abundant in different terrestrial ecosystems. Ant diversity tends to peak in tropical regions and decreases with increasing latitude and altitude (Guenard, 2013). Ants are an influential and important group of organisms in many ecosystems (Bestelmeyer & Wiens, 1996; Guenard, 2013), and their ecological role includes interactions with other organisms, such as bacteria, fungi, plants, other arthropods and vertebrates (Guenard, 2013). As a result, ants may influence the survival and control of other species (Guenard, 2013). In addition, ants are involved in different trophic levels as decomposers, detritivores, herbivores, predators and mutualists (de Castro Solar et al., 2016; Del Toro, Ribbons, & Pelini, 2012). As such, ants facilitate decomposition, nutrient cycling, pest control, seed dispersal, seed germination and pollination (Del Toro et al., 2012; Sanders & Platner, 2007). In decomposition processes, ants break down leaf litter for onward processing by other organisms (de Castro Solar et al., 2016; Del Toro et al., 2012; Rosado et al., 2012; Sanders & Platner, 2007).

Ants are used as bioindicators of ecological change (Munyai & Foord, 2015a; Read & Andersen, 2000; Wang, Strazanac, & Butler, 2000) because they are abundant, easy to sample and respond to changing environments at small spatial scales. They also play an important role in the establishment of food chains and are one of the well-studied groups of social insects (Read & Andersen, 2000; Wang et al., 2000). In many terrestrial ecosystems, ants have been used as bioindicators for assessment of restoration success after mining (Andersen, 1997a), livestock grazing (Nash et al., 2004), effect of disturbances in forests and grasslands (de Castro Solar et al., 2016; King, Andersen, & Cutter, 1998) and the effect of different land uses (Attwood, Maron, House, & Zammit, 2008; Bestelmeyer & Wiens, 1996). In addition, ants are used to assess soil functioning in rural environments (De Bruyn, 1999), the effect of fire (Parr, Robertson, Biggs, & Chown, 2004), logging practices (Andersen, 1997a), alien plant invasion (Lenda, Witek, Skórka, Moroń, & Woyciechowski, 2013) and pesticide use (Matlock & de la Cruz, 2003).

Ants are sensitive to ecological change, and habitat disturbance affects them enormously because they live and forage in the ground (Attwood et al., 2008; Schoeman & Foord, 2012; Wang et al., 2000).

Furthermore, ant activities are influenced by the structure, type and complexity of vegetation (Schoeman & Foord, 2012). Habitat disturbance may be associated with the removal of vegetation at ground level or invasion by alien plants (Attwood et al., 2008; Niba & Mafereka, 2015), both of which have serious implications on ant communities. Alien plants are known to outcompete indigenous plants, which are the main food resource for ants (Lenda et al., 2013). In addition, alien plants alter natural habitats and cause changes in food resources (Fork, 2010; Litt, Cord, Fulbright, & Schuster, 2014) resulting in the decrease in the abundance and richness of ant species (Litt et al., 2014). Changes in the habitat condition are not suitable for some ants, for example, the diversity of herbivorous ants may decrease in invaded habitats relative to natural habitats (Litt et al., 2014). Predator ants do not depend on native plants for food but invasion of alien plants may affect them through the decrease in prey species (Lenda et al., 2013; Litt et al., 2014). Many ant species forage on leaf litter and on vegetation (Parr et al., 2004). The abundance and diversity of ants are often positively correlated to habitat heterogeneity (Lassau & Hochuli, 2004). As such, alien invasive plants may affect some ant species, for example, myrmecochory (Litt et al., 2014).

The Sandstone Sourveld is an endemic savanna ecosystem occurring in KwaZulu-Natal (also called the KwaZulu-Natal Sandstone Sourveld, KZNSS) in South Africa. Many parts of the eThekwini Municipal area lie in this ecosystem, which is also part of the Maputaland-Pondoland-Albany biodiversity hotspot. This biodiversity hotspot consists of more than 7,000 plant species, with 25% of the species being unique to the region (Van Wyk & Smith, 2001). The KZNSS has received considerable research attention in the recent past (for example, Buhrmann, Ramdhani, Pammenter, & Naidoo, 2016; Drury et al., 2016; Naicker, Rouget, & Mutanga, 2016), which may partly be driven by the ecosystem's status as threatened and partly because of global trends of integrating the environment in urban planning (Boon et al., 2016; Roberts et al., 2012; Shih & Mabon, 2017). Although the importance of the KZNSS is understood better in terms of vascular plant species, most of the area's biodiversity, including invertebrates, is not known, which impacts negatively on management of the ecosystem (Rouget, O'Donoghue, Taylor, Roberts, & Slotow, 2016).

The aim of this study was to determine ant diversity in the Tanglewood and Giba Gorge Reserves. We sought to (a) determine the effect of alien plant invasion on ant species diversity and distribution in different vegetation types; (b) investigate the effect of season on ant assemblages; and (c) determine the effect of alien plant invasion on functional groups of ants. We hypothesise that ant diversity and functional groups are affected by the presence of alien plants. We expect to find lower ant diversity in the disturbed grassland and greater ant diversity in an intact grassland and the forest.

2 | MATERIALS AND METHODS

2.1 | Study sites

The study was conducted at two sites located in eThekwini Municipality, KwaZulu-Natal Province, South Africa. Human population density in the eThekwini Municipal area is approximately 1,644 per km². Tanglewood Nature Reserve (29°62.574'S, 30°40.330'E; 440 m above sea level) is a 70 ha privately owned property located in the Pinetown area. Giba Gorge Nature Reserve (29°49.628'S, 30°46.916'E; 519 m above sea level), which is jointly managed by the eThekwini Municipality and the Hillcrest conservancy, covers 72 ha of a predominantly grassland/savanna ecosystem of various elements (Figure 1). Tanglewood and Giba Gorge have relatively intact grassland, patches of riverine and scarp forests and a disturbed grassland that is a mosaic of natural/secondary grasslands resulting from the previous conversion to eucalypt and pine plantations. The disturbance was because of alien plant invasion. Approximately 10%-50% of the grassland in both reserves consists of patches of alien invasive plants, such as, Lantana camara L., Eucalyptus grandis W. Hill ex Maiden, Solanum mauritianum Willd ex Roth, Chromolaena odorata (L.) R.M King & H. Rob, Pinus elliottii Engelm, Acacia mearnsii De Wild, Tithonia diversifolia (Hemsl) A. Gray, Senna didymobotrya (Fresen.) H.S. Irwin & Barneby and Canna indica L.

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The vegetation is classified as KwaZulu-Natal Sandstone Sourveld (KZNSS), which is dominated by tall and short grasses, such as, *Aristida junciformis* Trin. & Rupr, *Diheteropogon amplectens* (Nees) Clayton, *Digitaria eriantha* Steud and *Monocymbium ceresiiforme* Stapf. The KZNSS experiences high rainfall in summer and dry conditions in winter, most rain falls between October and March with a mean annual rainfall of 700 to 1,200 mm (Mucina & Rutherford, 2006). Midday temperatures range from 16 to 25°C in winter and 23 to 33°C in summer (Mucina & Rutherford, 2006). The underlying geology is described as Ordovician Natal group sandstones that are overlain by shallow, nutrient-poor sandy soils (Mucina & Rutherford, 2006).

2.2 | Ants sampling

Ants were sampled using pitfall trapping, which is the most effective and widely used method for sampling ground-dwelling arthropods (Samways, McGeoch, & New, 2010). Pitfall sampling collects a large number of specimens compared to other methods used in collecting ground-dwelling arthropods (Gómez et al., 2003). Forest, intact grassland and disturbed grassland vegetation types were identified at each site. Each vegetation type was sampled in three replicates. Each replicate had ten pitfall traps laid in a 2 × 5 grid with 10 m spacing between adjacent pitfall traps as described by Munyai and Foord (2015b). Replicates were randomly located in each vegetation type and were separated by at least 300 m. Replicates in the disturbed grassland straddled patches of alien plants and secondary grassland as previously described for this vegetation type. Pitfall traps consisted of honey jars (64 mm diameter, 110 mm height, 500 ml volume) that were inserted each in a hole dug into the ground and the open end left



FIGURE 1 Location of the study sites in the eThekwini Municipal Area in KwaZulu-Natal Province, South Africa

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flush with the soil surface. Jars were guarter-filled with 50% propylene glycol solution for preserving collected specimens. Pitfall trap sampling was carried out in June and July 2016, which coincides with the dry season, and during the wet season in November and December 2016. Traps were removed after 5 days and taken to the laboratory where ground-dwelling ants were identified and counted. Fisher and Bolton (2016) was used to identify specimens to genus level while valid species names were confirmed using AntCat (http://www.antcat.org) and AntWeb (http://antweb.org). Some specimens were identified to genus level and then assigned to morphospecies or species level where possible. Some specieslevel identification was achieved by comparing species with those in the reference collection housed at the University of KwaZulu-Natal, Pietermaritzburg campus. Ant genera and species groups were categorised into five functional groups based on their general responses to environmental stress and disturbance, similar to Andersen (1997b)'s classification. Voucher specimens will be housed at the KwaZulu-Natal Museum in Pietermaritzburg, South Africa.

2.3 | Statistical analysis

Analysis of similarity (ANOSIM) and similarity percentage (Simper) with 9,999 permutations in PAST3 was used to determine if there were any significant similarities in species composition of ants among the vegetation types (Hammer, Harper, & Ryan, 2001). The differences or similarities between ant species composition across vegetation types were analysed using nonmetric multidimensional scaling (nMDS) in PAST3 with data ordered by replicates. The Bray-Curtis dissimilarity index was used for nMDS and ANOSIM analysis. Individual-based rarefactions and extrapolation curves were used to measure sampling effort.

Abundance was defined based on relative frequency (i.e., how many times the different morphospecies were registered in the pitfall traps) and not on the number of individuals collected because it minimises the bias caused by the presence of ant species that forage in groups. The relative frequency of each species in each vegetation type was calculated using the equation $f(\%) = F_i \times 100/F_t$ where F_i is the number of occurrences of a given morphospecies in each vegetation type and F_{+} is the total number of occurrences in each vegetation type (Lutinski et al., 2015).

To estimate species richness across vegetation types, the Incidence-based Coverage Estimator (ICE) was computed in EstimateS version 9.1.0 (Colwell, 2013). Individual-based rarefaction curves were computed in iNEXT online (Chao & Hsieh, 2016). Interpolation and extrapolation of ant incidences were based on Hill's numbers that integrate species richness and species abundance (Chao et al., 2014). The 95% confidence intervals were obtained by bootstrap method based on 200 replications (Chao & Hsieh, 2016). Sampling efficiency was estimated by computing the bootstrap, Chao2 and ICE estimators in EstimateS. This helps in determining if the sampling effort was sufficient and if all the species were sampled.

To determine whether there were differences in species occurrences across vegetation types at each site or season, a generalised linear model with Poisson distribution and log link function was used (Quinn & Keough, 2002). Generalised linear models were run using SPSS version 25 (IBM Corp, 2017). All statistical analyses used a significance level of 0.05. Data were square-root transformed to lessen the weight of the most abundant species. Values are expressed as the mean and standard deviation (±SD).

3 | RESULTS

In total, 2,577 occurrences from 54 species or morphospecies in 22 genera and five subfamilies were recorded in three vegetation types at the two sites during the wet and dry seasons (Table 3). Sample coverage for the whole survey ranged from 0.96 to 0.99 (Table 1). The Myrmicinae (27 species, 85% of total occurrences, from seven genera) was the most dominant and species-rich subfamily, followed by the Ponerinae (13 species, 8% of total occurrences, and from eight genera) and the Formicinae (10 species, 5% of the total occurrences, from 10 genera). The Dolichoderinae was less common and a species-poor subfamily (two species, <1% of the total occurrences, and one genus) while the Dorylinae had three species from two genera that made up 0.0027% of the total occurrences. With 1,349 occurrences, the disturbed grassland had more specimens followed by an intact grassland with 794 occurrences and a forest with 434 occurrences (Table 3). However, the intact grassland was the richest vegetation type with 40 species followed by the disturbed grassland with 27 species and the forest with 22 species (Table 3).

The species richness estimators (Chao2, ICE and bootstrap) consistently showed a greater number of species for both sites and all vegetation types than was observed (Table 1). Only in the disturbed grassland at Tanglewood was the observed and estimated species richness similar; elsewhere, Chao 2 and ICE showed much greater values than the observed number of species. Sampling efficiency based on bootstrap estimated that species richness was greater in the disturbed grassland (90.4) and forest (90.3) than in the intact grassland (85.1) in Tanglewood. In Giba Gorge, sampling efficiency was greater in an intact grassland (87.7) followed by the disturbed grassland (86.4) and the forest (72.9; Table 1).

Pheidole sp.2 (megacephala gp), Myrmicaria sp.1 and Lepisiota sp.1 (capensis gp) occurred in all three vegetation types. Pheidole sp.2 (megacephala gp) (62.3%), Pheidole sp. 3 (15%) and Myrmicaria sp.1 (6.2%) were the most abundant species in the disturbed grassland (Table 3). Pheidole sp.2 (megacephala gp) (50%), Leptogenys schwabi (18%), Myrmicaria sp.1 (8.4%) and Tetramorium sp.1 (squaminode gp) (6.3%) were the most abundant species in the forest. In an intact grassland, Pheidole sp.2 (megacephala gp) (48%) and Myrmicaria sp.1 were the most abundant species (Table 3). Thirteen species (24%) were found in the three vegetation types, eight (14%) were only found in two vegetation types and 33 (61%) were found in one vegetation type. Of these species, 21 (38%) were found only in an intact

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TABLE 1 Observed (Obs) number of species, occurrences (total number of individuals of all species), richness estimators (Chao2, ICE and bootstrap) and sample coverage of each vegetation type from Tanglewood and Giba Gorge Reserves

Vegetation types	Obs	Total occurrences	Chao 2	ICE	Bootstrap	Sample efficiency based on bootstrap	Sample coverage
Tanglewood							
Disturbed grassland	19	982	21.1	20.7	21.01	90.4	0.99
Forest	14	203	17.4	22.9	15.5	90.3	0.97
Intact grassland	20	397	31.8	28.1	23.5	85.1	0.98
Giba Gorge							
Disturbed grassland	16	369	18.7	23.7	18.5	86.4	0.98
Forest	14	223	21	32.4	19.2	72.9	0.96
Intact grassland	33	403	42.4	37.1	37.6	87.7	0.98

Note. ICE: incidence-based coverage estimator.

grassland, 5 (9%) were found in the forest only and 7 (13%) were found in the disturbed grassland.

Individual-based species rarefaction and extrapolation curves for vegetation types in Tanglewood and Giba Gorge reserves were slow to reach an asymptote. Ground-dwelling ant species richness peaked in the intact grassland in Tanglewood and Giba Gorge while the forest had significantly lower species richness in both reserves (Figure 2). Based on predicted species richness in the vegetation types in Tanglewood, the extrapolation curves suggest an increase in species richness with increasing number of individuals in the intact grassland and forest (Figure 2). In Giba Gorge, the extrapolation curves suggest a considerable increase in species richness with increasing number of individuals across all vegetation types (Figure 2). The wet season was associated with high species richness of ants compared to the dry season in both sites (Figure 3).

The nonmetric multidimensional scaling (nMDS) plot showed similarities in species composition of ants among disturbed grassland, forest and intact grassland (Figure 4). Intact grassland and a disturbed grassland had similar species composition compared to that of the forest. The similarity percentage indicated that the intact and disturbed grassland had similar species. The overall percentage of similarity was higher when the disturbed and intact grassland were compared in Tanglewood and Giba Gorge Nature Reserves (Table 2).

Greater occurrences of ants were recorded in the disturbed grassland (49.05 \pm 36.2) than in the forest (14.5 \pm 8.2) and intact grassland (19.8 ± 10.5) in Tanglewood (χ^2 = 5.91; df = 2; p < 0.05). However, occurrences of ants were similar across disturbed grassland (23.06 ± 12.4) , forest (13.9 ± 6.2) and intact grassland (12.2 ± 5.2) vegetation types in Giba Gorge ($\chi^2 = 2.90$; df = 2; p > 0.05). Observed $(\pm SD)$ species richness of ground-dwelling ants in the forest (14 ± 2) was lower than that recorded in an intact grassland (20 \pm 3) and disturbed grassland (19 ± 3) in Tanglewood. In Giba Gorge, species richness was greater in an intact grassland (33 \pm 2) than in the forest (14 ± 2) and disturbed grassland (16 ± 2) . The wet season had greater occurrences of ants than the dry season in Tanglewood ($\chi^2 = 6.57$; df = 1; p < 0.05) but occurrences were similar between seasons in Giba Gorge (χ^2 = 1.58; df = 1; p > 0.05). Species richness of grounddwelling ants was greater in the wet (27 ± 3) than dry season (19 ± 2) in Tanglewood. In Giba Gorge, species richness of ground-dwelling ants was significantly greater in the wet than dry season (i.e., 38 ± 3 and 19 ± 1 species, respectively). ANOSIM results showed significant differences in the ant communities among vegetation types at both sites (Giba Gorge: p < 0.01, R = 0.69; Tanglewood: p = 0.011, R = 0.47).

Opportunists were the most diverse functional group with 17 species or morphospecies (31% of the total richness), followed by specialist predators (13 species or morphospecies; 24% of the total







FIGURE 3 Individual-based rarefactions (solid lines) and extrapolation (dashed lines up to double reference sample size) of ant diversity based on Hill numbers (q = 0, 1, 2) for the dry and wet seasons in (a) Tanglewood and (b) Giba Gorge. The 95% confidence intervals (shaded regions) were obtained by bootstrap method based on 200 replications. Reference samples are denoted by symbols (triangle = wet season and a circle = dry season) [Colour figure can be viewed at wileyonlinelibrary.com]

richness), cryptic species (10 species or morphospecies; 19% of the total richness); generalised Myrmicinae (eight species or morphospecies; 14% of the total richness), surbordinate Camponotini (four species or morphospecies; 7% of the total richness) and tropical specialists (two species or morphospecies; 4% of the total richness)



FIGURE 4 Nonmetric Multidimensional Scaling (nMDS) of epigaeic ant assemblages in three vegetation types in Tanglewood (a) and Giba Gorge (b). Open circles represent disturbed grassland, triangles represent forest and solid squares represent intact grassland

(Figure 5). Generalised Myrmicinae represented a greater proportion of ants in the disturbed grassland (90%) compared with intact grassland (79.5%) and the forest (60%) in Tanglewood (Figure 6). Giba Gorge showed a similar trend as generalised Myrmicinae represented a greater proportion of ant occurrences in disturbed grassland (87%) compared with intact grassland (71%) and the forest (62%) (Figure 6). Specialised predators were more abundant in the forest in both Tanglewood (23.6%) and in Giba Gorge (17.9%).

4 | DISCUSSION

Ant species richness recorded in this study was 54 species or morphospecies from 22 genera, this is comparable to a previous study, and for example Munyai and Foord (2012) which employed similar pitfall trap sampling and recorded 78 species in 28 genera.



FIGURE 5 Species richness and proportion of functional groups of ants in Tanglewood and Giba Gorge Reserves

TABLE 2Overall similarity of epigaeic ant species compositionin the forest, disturbed grassland and intact grassland inTanglewood and Giba Gorge Reserves

Vegetation type comparison	Overall similarity (%)					
Tanglewood						
Disturbed grassland versus Forest	21.1					
Disturbed grassland versus Intact grassland	48.1					
Intact grassland versus Forest	30.8					
Giba Gorge						
Disturbed grassland versus Forest	29.9					
Disturbed grassland versus Intact grassland	38.3					
Intact grassland versus Forest	31.8					

However, the number of species that we found is lower than the 92 species recorded in the Maloti-Drakensburg in KwaZulu-Natal (Bishop, Robertson, Rensburg, & Parr, 2014). The latter study found high diversity of ants probably because of an intense sampling effort that spanned over 7 years, whereas the present study was conducted over 1 year in six sites. The Myrmicinae was the most

(a)



FIGURE 6 Functional group composition of ants in the vegetation types in (a) Tanglewood and (b) Giba Gorge. The functional groups are CS: cryptic species; GM: generalised Myrmicinae; OPP: opportunists; SC: subordinate Camponotini; SP: specialised predator; TCS: tropical climate species

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diverse subfamily followed by the Ponerinae and the Formicinae. The Myrmicinae comprises of generalist species and occurs abundantly in major vegetation types across major geographic regions (Ant Web, 2017; Sonune & Chavan, 2016). These observations conform to findings from other studies (e.g., Costa-Milanez et al., 2014; Munyai & Foord, 2015a). *Pheidole, Myrmicaria* and *Tetramorium* were the genera with most ant occurrences across disturbed grassland, forest and intact grassland in Tanglewood and Giba Gorge Reserves. These genera are abundant and speciose in several ecosystems because they are pioneer species and have great ability to adapt and diversify into different ecological niches (Achury, Chacón de Ulloa, & Arcila, 2011; Costa-Milanez, Lourenco-Silva, Castro, Majer, & Ribeiro, 2014).

The occurrences of ants in Tanglewood and Giba Gorge Reserves can be explained using the intermediate disturbance hypothesis, which states that species diversity and abundance tend to be greater under moderate levels of disturbance (Bongers, Poorter, Hawthorne, & Sheil, 2009). Disturbance creates macro-environments with suitable resources and habitat conditions, which allow for some species to persist and dominate (Bongers et al., 2009; McCabe & Gotelli, 2000). Berman, Andersen, Hély, and Gaucherel (2013) found that ants were more abundant in disturbed habitats than undisturbed habitats. Disturbed grassland in Tanglewood and Giba Gorge Reserves consisted of patches of alien invasive plants, which are responsible for modifying habitats, food resources and biotic interactions and provide optimum and suitable resources to grounddwelling arthropods (Niba & Mafereka, 2015; Niba & Yekwayo, 2016). The impact of alien plants on insect assemblages is not always negative because alien plants may provide nesting and foraging sites (Harris, Toft, Dugdale, Williams, & Rees, 2004), or may be dominated by arboreal ants which may further enhance the diversity of these areas, as some species that nest in trees also forage on the ground. According to Harris et al. (2004), alien plants may have more food resources and breeding grounds for insects, such as generalist ant species than indigenous vegetation. However, Samways, Caldwell, and Osborn (1996) reported that some alien plants may have a detrimental effect on abundance of ground-dwelling arthropod assemblages. The effect of alien plants on ground-dwelling arthropods also depends on the intensity of the invasion (Niba & Mafereka, 2015). Minimal or moderate invasion intensity by alien plants has lower or no impact on the abundance of ground-dwelling arthropods, such as Xysticus natalensis, Hippasa australis, Caraminara sp., Crematogaster sp. and Pheidole sp. (Niba & Mafereka, 2015).

Intact and disturbed grassland had greater ant species richness than the forest in both Tanglewood and Giba Gorge Reserves. Forests are characterised by high deposition of leaf litter on the ground, which influences resource availability, macroclimatic conditions and availability of nesting sites for ants (Silva, Frizzas, & de Oliveira, 2011). These forest conditions may have a negative effect on ant species diversity. In addition, pitfall traps are best at sampling arthropods on bare ground, as such, high amounts of leaf litter on the ground in the forest might have resulted in fewer individuals being recorded. Yekwayo, Pryke, Roets, and Samways (2016) found

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that grasslands supported higher arthropod (particularly ants) abundance and richness compared to forests, and arthropods made up 60% of the sampled individuals in forest and grassland habitats. Ant diversity may decline sharply in forest habitats because ants do not do well in shaded environments (Bestelmeyer & Wiens, 1996). Ants' body temperature decreases with decreasing air temperature, this reduces ants foraging activities, which may explain the decline in ant diversity and richness in shaded environments (Porter & Tschinkel, 1987). Furthermore, ants prefer warm climatic conditions and forage in sites with low vegetation (Kyerematen, Owusu, Acquah-Lamptey, Anderson, & Ntiamoa-Baidu, 2014), which probably explains the high species richness in an intact grassland and disturbed grassland.

There was considerable overlap of ant species across the forest, intact grassland and disturbed grassland. The three vegetation types had few unique species, most species were common across the disturbed grassland, forest and intact grassland. The level of similarity in ant composition between the sites was very high. Pheidole sp.2 (megacephala gp), which is associated with warm tropical and subtropical environments, was abundant in disturbed grassland. Pheidole sp.2 (megacephala gp) is a generalist species, it is not surprising that this species was more abundant in the disturbed vegetation type as generalist species have broad diet and are able to colonise and persist in disturbed sites (Fotso Kuate, Hanna, Tindo, Nanga, & Nagel, 2015). Leptogenys schwabi, a member of the Ponerinae, occurred in the forest and disturbed grassland only; it was more abundant in the forest at both sites. Leptogenys schwabi is associated with riverine and eastern coastal belt forest of South Africa (Ant Web, 2017), which may explain its abundance in the forest.

The wet season was associated with high diversity of ants compared to the dry season in both sites. These results are in agreement with the findings of Keroumi, Naamani, Soummane, and Dahbi (2012) who reported greater abundance and higher species richness of ants in the wet than dry season in an Argan forest of Morocco. Munyai and Foord (2015b) reported that ground-dwelling ants are intolerant of cold conditions and are more active and abundant in the wet than dry season. Activities of ground-dwelling ants are affected by food resource availability, temperature, moisture and solar radiation, whose influence declines in the dry season and increases in the wet season (Abhinandini & Venkatesha, 2013). In the wet season, the greater availability of food resources may reduce interspecific competition resulting in increases in ant abundance (Philpott, Perfecto, & Vandermeer, 2006). In addition, foraging activities of ground-dwelling ants are greater in the wet than dry season because the dry season is associated with cooler climate that forces many invertebrates to hibernate thus reducing their abundance in trap samples (Pinheiro, Diniz, Coelho, & Bandeira, 2002; Silva, Bieber, Corrêa, & Leal, 2011).

Generalised Myrmicinae had greater proportion of ground-dwelling ants in the disturbed grassland than in the forest and intact grassland. In addition, generalised Myrmicinae were the most dominant species in all vegetation types. Disturbance usually favours generalist ants because they have broad ecological requirements and can survive under disturbed and undisturbed habitat types and under wet and dry climatic conditions (Andersen, 1997b; Fotso Kuate et al., 2015). Andersen (1997b) reported that generalised myrmicines are sub-dominant to species from dominant dolichoderines. However, in the absence of species from dominant dolichoderines, the generalised myrmicines become competitively dominant and take over in different ecological niches. In the present study, the often dominant dolichoderines were not recorded, which might explain the greater occurrence of generalist species. Generalised Myrmicinae comprised of genera, such as Pheidole, Myrmicaria and Crematogaster. The dominance of these genera is consistent with other studies that demonstrated that these groups are abundant in many terrestrial ecosystems (Achury et al., 2011: Costa-Milanez et al., 2014: Rosado et al., 2012). Opportunists were the most diverse functional group. These observations conform to findings by Fotso Kuate et al. (2015), who found opportunists to be the most diverse functional group in disturbed and undisturbed vegetation types in Southern Cameroon. Ant species from this functional group are characterised by wide geographic ranges and have unspecialized diets (Andersen, 1997b), which might explain their high species richness in Tanglewood and Giba Gorge.

5 | CONCLUSION

Diversity of ants in KwaZulu-Natal Sandstone Sourveld was influenced by vegetation type. The intact grassland had greater diversity of ants than the forest and the disturbed grassland in both Tanglewood and Giba Gorge Reserves. However, the disturbed grassland supported higher ant occurrences than an intact grassland and forest. These results suggest that grassland disturbance by alien plant invasion provides environmental heterogeneity that may increase occurrences of ants but does not promote the diversity of ants, which lends support to the hypothesis that diversity and functional groups of ants are affected by the presence of alien plants. To promote greater diversity of ants in the KwaZulu-Natal Sandstone Sourveld, the disturbed grassland should be managed in order to reduce the areal extent of alien invasive plants.

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APPENDIX A

Taxon	Functional group	Disturbed grassland	Prf	Forest	Prf	Intact grassland	Prf
Formicidae							
Dolichoderinae							
Technomyrmex sp.1	OPP					1	0.1
Technomyrmex pallipes	OPP					3	0.4
Dorylinae							
Aenictus rotundatus	TCS					2	0.3
Parasyscia sp.1	SP					3	0.4
Parasyscia sp.2	SP					2	0.3
Formicinae							
Camponotus cinctellus	SC	2	0.1	2	0.5	5	
Camponotus maculatus	SC	17	1.3	1	0.2	1	0.1
Camponotus rufoglaucus	SC				14	1.8	
Camponotus sp.1	SC					1	3.5
Lepisiota sp.1 (capensis gp.)	CS	12	0.9	20	4.7	7	0.9
Lepisiota sp.3 (capensis gp.)	CS	2	0.1				
Lepisiota sp.4 (capensis gp.)	CS		2	0.5			
Nylanderia sp.1	OPP	11	0.8			32	4.0
Nylanderia sp.2	OPP	5	0.4				
Polyrhachis schistacea	TCS					2	0.3
Myrmicinae							
Crematogaster sp.1	GM					27	3.3
Crematogaster sp.2	GM			3	0.7	3	0.4
Crematogaster castenea	GM	4	0.3				
Monomorium sp.1 (monomorium gp.)	GM	1	0.1	1	0.2	2	0.3
Myrmicaria natalensis	GM	85	6.3	36	8.5	74	9
Pheidole sp.1	GM	68	5.0	5	1.2	75	9.4
Pheidole sp.2 (megacephala gp.)	GM	843	62.3	217	50	383	48
Pheidole sp.3	GM	205	15			4	0.5
Pheidole sp.3 (megacephala gp.)	GM				36	4	
Pheidole sp.4	GM	1	0.1	2	0.5	10	1.3
Solenopsis sp.1	CS					1	0.1
Solenopsis sp.2	CS	5	0.4			4	
Solenopsis sp.3	CS	5	0.4	1	0.2	1	0.1
Strumigenys sp.1	CS					1	0.1
Tetramorium notiale	GM	6	0.4				
Tetramorium cf. setigerum	GM	9	0.7	2	0.5	5	0.6
Tetramorium sp.1 (squaminode gp.)	GM	11	0.8	27	6.3	4	0.5
Tetramorium sp.10 (similimum gp.)	CS	3	0.2	2	0.5		
Tetramorium sp.11	GM					2	0.3
Tetramorium sp.12	GM					2	0.3
Tetramorium sp.13	GM			4	0.9		
Tetramorium sp.2	GM					2	0.3

TABLE A1 Percentage relative frequencies (Prf) and Occurrences of ground-dwelling ants (Hymenoptera) across three vegetation types during the wet and dry seasons in Tanglewood and Giba Gorge Reserves

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TABLE A1 (Continued)

Taxon	Functional group	Disturbed grassland	Prf	Forest	Prf	Intact grassland	Prf
Tetramorium sp.3 (simillimum gp.)	CS	1	0.1	7	1.6	3	0.4
Tetramorium sp.4 (sericeiventre gp.)	GM				11	1.4	
Tetramorium sp.5	GM					5	0.6
Tetramorium sp.6	GM					1	0.1
Tetramorium sp.7	GM	1	0.1				
Tetramorium sp.8 (squaminode gp.)	GM		5	1.2			
Ponerinae							
Anochetus bequaerti	SP	2	0.1				
Bothroponera cavernosa	SP					3	0.4
Bothroponera sp.1	SP	17	1.3			15	1.9
Hypoponera sp.1	SP			5	1.2		
Leptogenys schwabi	SP	16	1.2	78	18		
Leptogenys nr attenuata	SP			1	0.2	20	2.5
Mesoponera nr sharpi	SP	10	0.7	8	1.9	26	3.2
Mesoponera sp.1	SP			5	1.2		
Mesoponera sp.2	SP	6	0.4				
Ophthalmopone sp.1	SP	2	0.1				
Plectroctena mandibularis	SP					1	0.1
Number of occurrences		1,349		434		794	

Note. The functional groups are CS: cryptic species; GM: generalised Myrmicinae; OPP: opportunists; SC: subordinate Camponotini; SP: specialised predator; TCS: tropical climate species.